

Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*

David A. Griffin^A, John L. Wilkin^B, Chris F. Chubb^C, Alan F. Pearce^D, and Nick Caputi^C

^ACSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia. email: David.Griffin@marine.csiro.au

^BNational Institute of Water and Atmospheric Research, New Zealand. Present address: Institute of Marine and Coastal Sciences, Rutgers University, NJ 08901, USA. email: wilkin@imcs.rutgers.edu

^CWestern Australian Marine Research Laboratories, Fisheries WA, PO Box 20, North Beach, WA 6920, Australia. email: cchubb@fish.wa.gov.au; ncaputi@fish.wa.gov.au

^DCSIRO Marine Research, PO Box 20, North Beach, WA 6920, Australia. email: Alan.Pearce@marine.csiro.au

Abstract. The return of *Panulirus cygnus* larvae to the coast of Western Australia after nearly a year at sea and its modulation by ocean currents were addressed with an individual-based larval-transport model. The simulations implied that offshore wind-driven transport of larvae is balanced by onshore geostrophic flow. Additional simulations revealed that vertical migration behaviour was essential to larval survival through its impact on advection. The six years simulated include two of high, two of low, and two of average puerulus settlement. The most robust interannual difference of the simulations was that, when coastal sea level was low and the Leeuwin Current was weak, more early-stage larvae were lost to the north and west under the influence of the wind. Conversely, many late-stage model larvae were carried south of the fishery in years when the Leeuwin Current was strong. The fraction of model larvae remaining or arriving offshore of the fishery and metamorphosing was essentially constant from year to year, so the variation in observed puerulus settlement was not explained by the model. The results imply that the nonadvective effects of fluctuations in the Leeuwin (e.g., on temperature and primary production) were primarily responsible for the high variation in natural settlement.

Introduction

The western rock lobster, *Panulirus cygnus*, is Australia's most valuable single-species fishery; annual catch between 1987 and 2000 ranged from 9200 to 14 500 t, and economic value from A\$170 to A\$380 million (Fig. 1). Recruitment to the fishery is well correlated with the rate of puerulus settlement 3 and 4 years earlier (Phillips 1986). Hence, monitoring puerulus settlement rate permits forecasting of the future catch of the fishery, providing an invaluable tool for fisheries management. The successful prediction of a record catch for the 1999–2000 season resulted from a combination of the two strong puerulus settlements of 1995 and 1996 (Fig. 1).

Research into environmental influences on the rate of puerulus settlement is motivated by the desire to distinguish natural from fishery-induced variations. To date, the work on *P. cygnus* has been mostly correlative. Pearce and Phillips (1988) found that coastal sea level at Fremantle was correlated with the rate of settlement. Caputi *et al.* (1996) found that onshore winter winds (as inferred from rainfall) increased the correlation. Recently, Caputi *et al.* (2001 this issue) found that sea-surface temperature was also correlated with settlement. These correlations are evident in

the time series of puerulus settlement and environmental variables (Fig 1).

Many physical processes potentially drive the correlation of puerulus settlement with coastal sea level at Fremantle and the regional sea-surface temperature. Both are indices of the strength of the Leeuwin Current, which flows southward along the south-west Australian continental slope (Cresswell and Golding 1980), principally from April to September, when opposing winds (Fig. 1) are weakest (Godfrey and Ridgway 1985). The shallow (200-m) current is fed from both offshore and the north and brings warmer, less saline, low-nutrient tropical waters southward. Its flow is highly unstable. Anticyclonic eddies of warm waters are commonly shed, sometimes in association with cyclonic eddies seaward of the current (Andrews 1983; Pearce and Griffiths 1991). Phytoplankton density is relatively high in these anticyclonic eddies (Plate I), despite the low densities in the core of the Leeuwin, suggesting that they contain a significant proportion of shelf waters, which are relatively productive during winter (C. Pattiaratchi and A. F. Pearce, unpublished). Current velocities up to 1.4 m s^{-1} associated with the eddy field greatly exceed the time-mean surface flow field, which precludes accurate estimation of the latter (Hamon and Cresswell 1972). The Leeuwin Current is

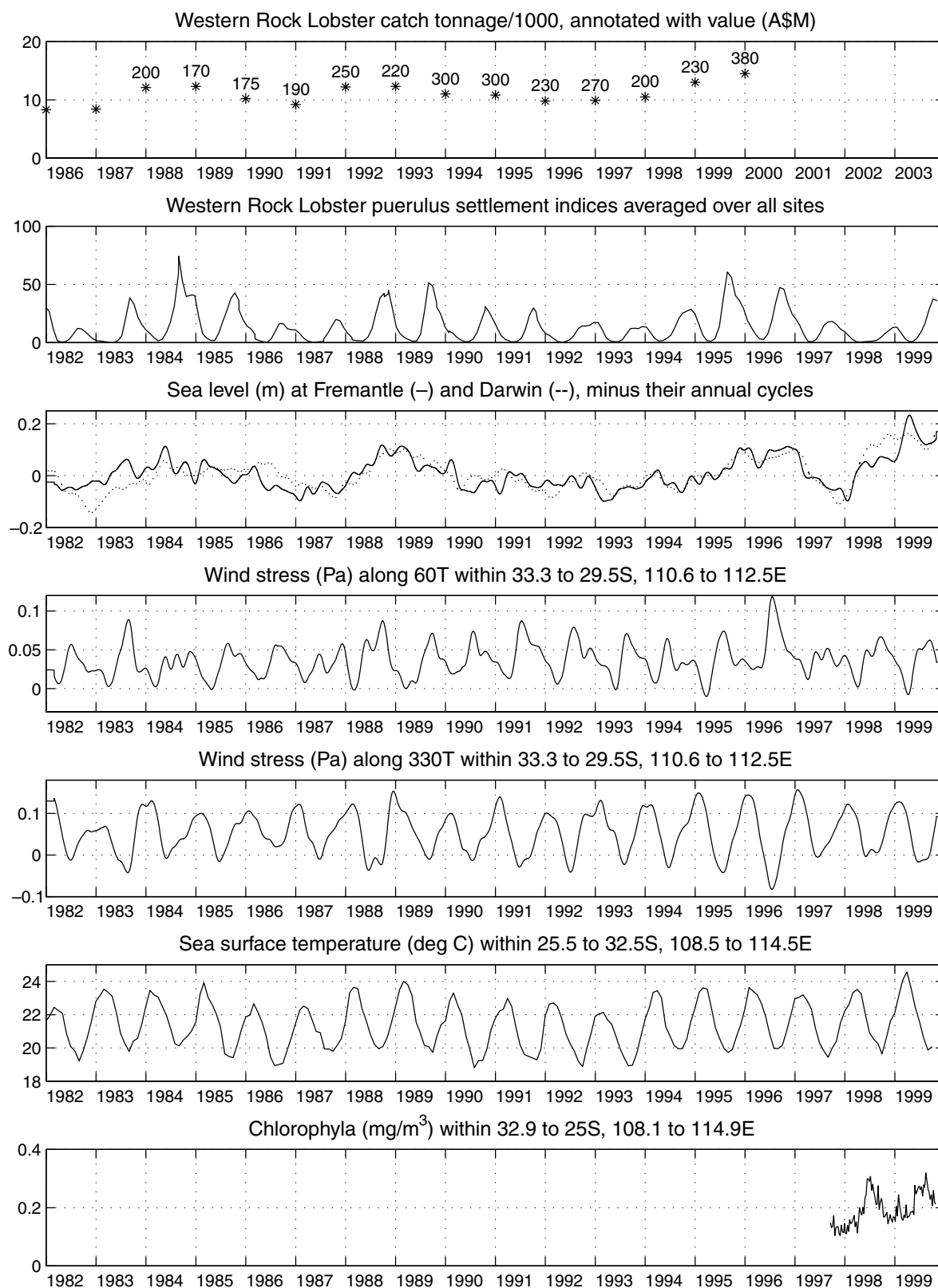


Fig. 1. Time series of (i) annual tonnage and value of commercial catches of *P. cygnus*; (ii) monthly puerulus settlement indices averaged over all monitoring sites; (iii) 60-day averaged sea level (minus the annual cycle and inverse-barometer response) at Fremantle and Darwin harbours; (iv) onshore and (v) alongshore components of 60-day averaged NCEP/NCAR Reanalysis surface wind stress, averaged over the region indicated; (vi) Reynolds monthly averaged sea-surface temperature; and (vii) 8-day composite SeaWiFS estimates of surface chlorophyll a.

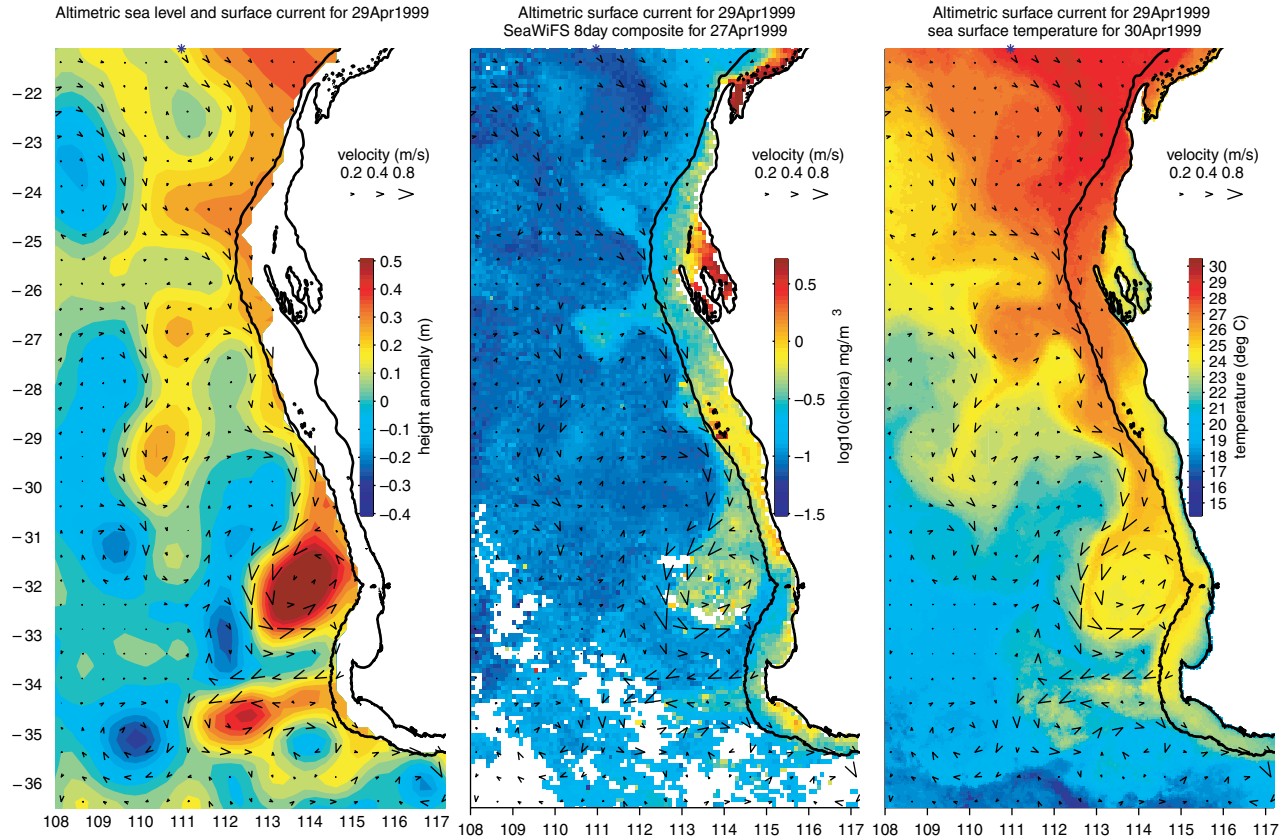


Plate I. Maps of the study region comparing (i) the sea-level height anomaly measured by satellite altimeters (ii) chlorophyll-a concentration measured by SeaWiFS imagery of ocean colour, and (iii) sea surface temperature measured by NOAA satellite AVHRR thermal imagery. Arrowheads in all panels show the geostrophic surface current inferred from the sea-level field. The 200-m isobath is shown.

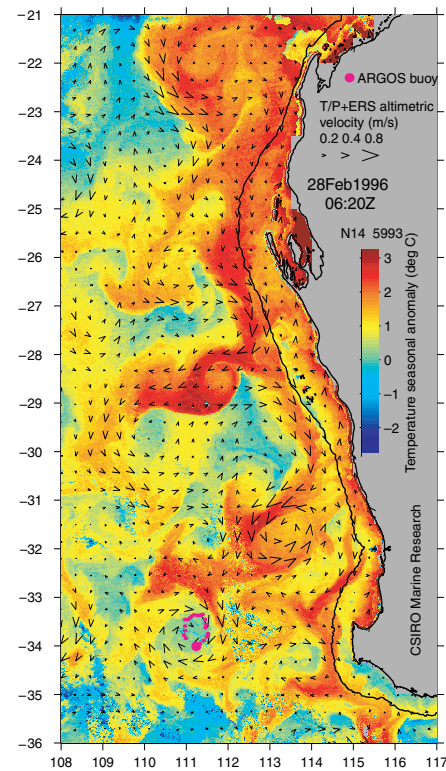


Plate II. Comparison of altimetric current velocity estimates (arrowheads) with trajectory, at 6-h intervals over 5 days, of Argos-tracked WOCE SVP surface drifter (magenta) and sea surface temperature (SST) anomaly. Altimetric velocity has time-mean velocity from the ACOM global model added. SST anomaly is the difference of SST from the CSIRO Atlas of Regional Seas (CARS) seasonal (mean plus annual and semiannual), climatological hydrographic SST field. 200-m isobath shown.

especially strong when the Indonesian throughflow is strong (Schiller *et al.* 2000), which happens when sea level in the western equatorial Pacific is higher than usual, as happens during La Niña. The reverse occurs during El Niño, so Fremantle sea level is strongly influenced by the sea level to the north, for example as measured at Darwin (Fig. 1), while also being a local indicator of the Leeuwin Current.

Three major questions must be addressed: why a strong Leeuwin Current should result in greater puerulus settlement, which of the covarying environmental variables is the dynamically important one, and, first of all, how larvae return to the coast after nearly a year at sea, despite the mean eastward and southward flow. Chittleborough and Thomas (1969) found many mid-stage larvae as far west as 109°E in February 1968 and reasoned that this offshore transport resulted because the early-stage larvae remained near the surface, where they would be transported as a result of summer south-easterly winds. Chittleborough and Thomas estimated that winds of November 1967–February 1968 could have transported larvae 280 miles westward and speculated that later-stage larvae would return to the coast if they avoided surface waters. Phillips *et al.* (1978) found larvae as far west as 100°E and as far north as 21°S, but it was unclear whether these widely distributed larvae could return to the coast. By then, the existence of a mean geostrophic flow back towards the coast was no longer in doubt, but its strength and persistence were unknown, as was the extent to which larvae could successfully exploit it to return to the coast.

Although much more is now known about the regional oceanography and the vertical and spatial distribution of larvae, no quantitative test of the basic larval advection hypothesis of Chittleborough and Thomas (1969) has been conducted. We therefore developed a quantitative biophysical model of larval transport and examined the role of interannual variability of winds and large- to mesoscale ocean currents in explaining observed variability of puerulus settlement, through large-scale *advective* processes.

Methods

Larval advection models can be either Eulerian, like that of Chiswell and Booth (1999), or Lagrangian, like those of Polovina *et al.* (1999) and Incze and Naimie (2000), who modelled, respectively, transport of the larvae of *Jasus edwardsii*, *Panulirus marginatus*, and *Homarus americanus*. We have chosen the Lagrangian (or individual-based) method, wherein the positions of individual model larvae are advanced at regular intervals (8 h in our case) by a displacement that depends on an estimate of the water-velocity field at the depth and location of each larva at each time. Larvae make diel vertical migrations, according to their age, but do not swim horizontally. The displacement of pueruli, however, includes swimming. We used a 4th-order Runge-Kutta integration scheme (Hofmann *et al.* 1991) to ensure that model larvae did not diverge from regions of circular flow.

Hatching

Mature *P. cygnus* begin to mate in late autumn, and the first-stage larvae hatch throughout the summer from November to February with a peak in January (Chubb 1991). Incubation is faster at higher temperature (Aldrich 1967); most females produce two broods per season (Chubb 1991).

We modelled the hatching of larvae by releasing a constant number of model larvae every five days from 1 November to 28 February at a line of locations along the outer continental shelf of Western Australia between latitudes 27°S and 34°20'S, where adults are concentrated.

Vertical migration

Vertical migration behaviour of *P. cygnus* larvae is well known because of extensive field sampling (Ritz 1972; Phillips *et al.* 1978; Rimmer and Phillips 1979; Rimmer 1980; Phillips and Pearce 1997), although the controlling factors are unknown. All larval stages avoid light and are principally found near the surface at night and at depth between sunrise and sunset. The later stages make greater diurnal migrations than the early stages and only come to the surface on the darkest of nights, and then only if winds are relatively weak.

We modelled vertical migration (see Fig. 2) by dividing observed behaviours into three classes. Model larvae graduated from one class to the next as they reached critical ages. In the vertical dimension, we distinguished three depth strata: upper (0–10 m), mid-depth (10–50 m), and deep (50–90 m). Early-stage (I–III, ages 0–50 d) larvae were in the upper layer at night (2100–0500; one model time step) and the middle layer by day (0500–2100; two model time steps). Mid-stage (IV–VI, ages 50–85 d) larvae descended to the deep layer by day. Late-stage (VII–IX, ages 85+ d) ascended to the surface layer only within three days on either side of a new moon; otherwise they ascended to the middle layer.

The puerulus stage

Much less is known about the puerulus stage than about larval stages, as few pueruli have been collected in plankton tows (Phillips and Pearce 1997). Pueruli are strong swimmers (Phillips and Olsen 1975) and do not feed (Lemmens 1994), suggesting that they are rarely sampled because they spend a short time as pueruli. In the laboratory, the swimming puerulus phase lasted only about a week (Lemmens 1994). Pueruli are caught in coastal collectors almost exclusively within two days of the new moon (Phillips 1975).

To compare our simulation results with observed puerulus settlement rates, we modelled the puerulus stage, despite uncertainty over triggers of metamorphosis, depth strata occupied by the puerulus, their swimming speed and duration, and settlement habitats. We used two metamorphosis scenarios: one in which all larvae metamorphosed as soon as they reached an age of 270 days and one in which metamorphosis occurred when larvae of age greater than 270 days first encountered the continental slope (depth < 2000 m) within three days of new moon. Once metamorphosed, model pueruli swam eastwards at $\mathbf{v}_{swim} = 0.1 \text{ m s}^{-1}$ plus the current velocity in the surface layer at night and in the middle layer by day. If they reached water shallower than 100 m within three days of new moon, they were counted as settling successfully. If currents carried them offshore, they were given one more month to settle, although this condition may not be realistic. Our modelling of the puerulus stage was a weakness, and the number settling in the model should be interpreted as an index of the number of late-stage larvae encountering the continental slope near new moon. The observed settlement rates exhibited high spatial and within-year correlation, however, so we suspect that *variability* of puerulus mortality may not be very high, in which case our approach is justified. Further, Caputi *et al.* (1996, this volume) demonstrated a substantial lag in the correlation of larval settlement rates and environmental

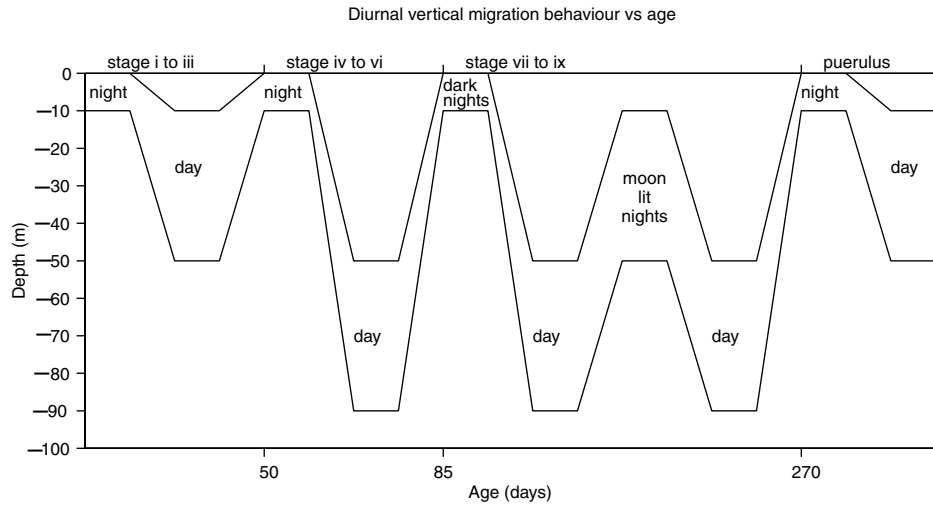


Fig. 2. Schematic of the model depth strata occupied by model larvae by night and day as a function of larval age.

variables, suggesting that conditions at the time of metamorphosis and settlement do not drive settlement variability.

Velocity fields

Estimates of the current velocity for advecting the larvae were not, for the work reported here, obtained from a hydrodynamic model of the region. Instead, we used an observation-based approach.

The advent of satellite altimetry permits estimation of the large-scale to mesoscale variability of surface currents by geostrophy, from maps of sea level η produced from a combination of satellite altimeter and coastal tide-gauge observations. The geostrophic, ‘altimetric’ velocity vector estimate $\mathbf{v}_{ga}$ is given by

$$f\mathbf{v}_{ga} = -g\nabla\eta \quad (1)$$

where f is the Coriolis parameter and g is the acceleration due to gravity. However, $\mathbf{v}_{ga}$ is incomplete as an estimate of the total current because (1) the time-mean of the sea level field could not be estimated accurately at a high spatial resolution, so the mean was removed; (2) wind-driven motions could not be diagnosed directly from sea level; and (3) small-scale and very transient non-wind-driven currents were not adequately resolved by the two existing (nadir-only viewing) altimeters.

Our larval advection model required estimates of the depth-averaged current $\mathbf{v}_1$, $\mathbf{v}_2$ and $\mathbf{v}_3$ within 0–10 m, 10–50 m, and 50–90 m. We estimated these by augmenting the altimetric estimate differently for each layer as follows:

$$\mathbf{v}_1 = \mathbf{v}_{m1} + \mathbf{v}_{altim} + \mathbf{v}_{Ek} + \mathbf{v}_{sfc} + \mathbf{v}_{rand} \quad (2)$$

$$\mathbf{v}_2 = \mathbf{v}_{m2} + \mathbf{v}_{altim} + \mathbf{v}_{Ek} + \mathbf{v}_{rand} \quad (3)$$

$$\mathbf{v}_3 = \mathbf{v}_{m3} + a\mathbf{v}_{altim} + \mathbf{v}_{rand} \quad (4)$$

where $\mathbf{v}_{altim}$ is a refinement of $\mathbf{v}_{ga}$ derived as follows:

Altimetric velocity $\mathbf{v}_{altim}$

The most energetic contributor to the total velocity is the (approximately) geostrophic, yearly- to weekly-varying component $\mathbf{v}_{altim}$ that we diagnosed from sea-level maps produced from combined

coastal tide gauge, European Space Agency Earth Resources Satellite (ERS), and (NASA-CNES) Topex/Poseidon satellite altimeter measurements. The Topex/Poseidon altimeter was launched in September 1992. We did not estimate velocities before then, largely for the sake of uniformity. For this study, we used the data until the end of 1998, and we note a gap in the availability of ERS data for 1994.

The sea-level mapping method was a modification of the method used by Le Traon and Hernandez (1992). Briefly, the subsatellite height estimates were optimally interpolated onto a 0.1758° (about 20-km) grid spanning 41.9°S to 21.1°S , 100.1°E to 124.9°E , every 5 days, with overlapping data windows of 25 days. These maps are anomalies about the 1993–1998 mean, because the present estimate of the geoid is not accurate enough to estimate the mean height field at 20-km resolution.

Coastal tide-gauge data and estimates of the sea-level anomaly at the shelf break were included in the sea-level mapping. We formed the shelf-break estimates by making the across-shelf height gradient (and hence the alongshore geostrophic current) a function of local and upstream (in the sense of coastal trapped wave propagation) alongshore wind stress. The other effect of doing so was to concentrate the height gradient associated with the Leeuwin Current over the continental slope, as indicated by field observations. The relationship of wind-driven shelf currents to local and remote wind forcing was established by a multiple-regression analysis similar to that of Griffin and Middleton (1991). Note that the remote winds are worthy of inclusion: tropical-cyclone-force winds as far north as 15°S make a significant contribution to the shelf current at Fremantle (33°S).

We estimated the Cartesian components u, v of $\mathbf{v}_{altim}$ from the sea-level height η maps by assuming a steady-state, frictional, cyclostrophic momentum balance

$$-fu = g\eta_y + uv_x + vv_y + C_D(u^2 + v^2)^{1/2}v/h \quad (5)$$

$$fv = g\eta_x + uu_x + vu_y + C_D(u^2 + v^2)^{1/2}u/h \quad (6)$$

where u and v are layer-averaged velocity components along the x and y axes, subscripts denote partial differentiation, $C_D = 5 \times 10^{-4}$ is a drag coefficient, and h is the layer thickness, estimated as $h = 150 + 150\eta$. To solve Eqs 5 and 6, we estimated the terms on the RHS using the Cartesian components of $\mathbf{v}_{ga}$ as approximate estimates of u and v . The effect of including the advective terms in Eqs 5 and 6 was to increase

the velocities of anticyclonic flow, and decrease the velocity of cyclonic flow, for equal height gradient. The effect of including the frictional terms was to make cyclonic eddies weakly convergent at the surface and anticyclonic eddies divergent. The combined effect was to make changes of typically 10% of the total.

For the deepest layer (see Eq. 4), we attenuated $\mathbf{v}_{altim}$ by $a = 0.8$, which is the average observed attenuation, at that depth, of anomalies of dynamic height in the study region (K. Ridgway, CSIRO, pers. comm.).

Open-ocean, wind-forced velocities $\mathbf{v}_{sfc}$ and $\mathbf{v}_{Ek}$

The effect of wind stress could straightforwardly be incorporated into Eqs 5 and 6. We took a more computationally efficient approach and approximated the total velocity in the upper two layers as the sum (see Eqs 2 and 3) of a (slowly varying) component primarily associated with pressure gradients and (more rapidly varying, but more spatially coherent) components associated with local wind forcing. We estimated the surface wind drift $\mathbf{v}_{sfc}$ as being 3.5% of the wind at 10 m height, rotated 20° left (see, e.g., Katz *et al.* 1994). Estimates of the 10-m wind at 12-h intervals were those of the NCEP/NCAR 40-year reanalysis on a 1.9° by 1.9° grid (Kalnay *et al.* 1996). These analysed wind estimates compared well with observed winds at Fremantle, although the strength of the diurnally varying sea breeze component was underestimated by about a half. We did not compare them with *in situ* observations offshore.

To estimate the time-dependent velocity $\mathbf{v}_{Ek}$ of an Ekman layer of constant thickness 50 m, we used the simple Pollard and Millard (1970) method, which simulates the damped inertial oscillations resulting from transient wind forcing. The model was forced with the NCEP/NCAR daily averaged wind stress, and we used a linear interfacial friction coefficient of 0.002 m s^{-1} .

Time-mean velocities $\mathbf{v}_{m1}$, $\mathbf{v}_{m2}$ and $\mathbf{v}_{m3}$

Finally, estimates of the geostrophic (*i.e.*, excluding the wind-driven component) mean velocity fields for 1993–1998 were required for the three model strata. For many regions, the climatological-average dynamic height fields estimated from historical hydrographic data serve this purpose. The present study region, however, has not been surveyed very intensively, and the value of the existing data for estimating the mean state is reduced because of the large amplitude of the transient eddy field. For all study regions, there are also the problems of selecting a level of no motion, and computing the height field over the continental slope. The best available estimate of the mean dynamic height field was that of the CSIRO Atlas of Regional Seas (CARS). We used this to estimate the mean velocities $\mathbf{v}_{m1}$, $\mathbf{v}_{m2}$ and $\mathbf{v}_{m3}$ at 0 m, 30 m, and 75 m depth, respectively, assuming a level of no motion at 300 m. Because 300 m may not, in fact, be the best choice for level of no motion, we assessed the impact of this choice by also computing the flows with respect to 1000 m and 2000 m.

Another estimate of the three-dimensional time-mean velocity field was derived from a new global ocean model, ACOM3, recently developed at CSIRO. This is essentially a finer-resolution ($1/3^\circ$ latitude by $1/2^\circ$ longitude) version of the model of Schiller *et al.* (2000), forced by 3-day averaged NCEP/NCAR and FSU atmospheric fluxes. We estimated the sub-Ekman-layer mean-velocity field for our model depth strata by averaging the ACOM3 estimates of the flow fields for 1992 to 1998 between 30 m and 60 m and 60 m and 100 m. We did not use the ACOM3 Ekman-layer response (either the mean or the transients) because it was not straightforward to separate it from the pressure-gradient-associated flows, which we estimated by altimetry and did not want to double-count.

Accuracy

We assessed the accuracy of our (middle-layer) velocity estimates by comparing them with the velocities of World Ocean Circulation Experiment Surface Velocity Program (WOCE SVP) drifting buoys and research vessel Acoustic Doppler Current Profiler (ADCP) data. Figure 3 shows that our estimates explained about half the total

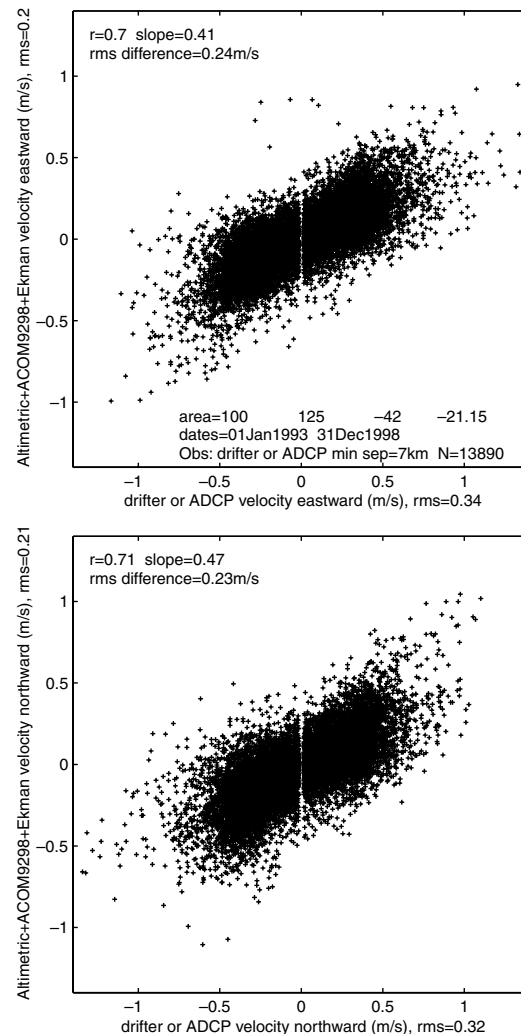


Fig. 3. Comparison of *in situ* measurements of current velocity with corresponding 'model' estimates. The observed eastward (upper panel) and northward (lower panel) velocity components are plotted along the *x* axis and comprise 13 519 WOCE drifter and 363 ADCP observations. The drifter velocities are those estimated at 6-h intervals by the WOCE SVP DAC from interpolated trajectories, excluding estimates within 7 km of each other. The drifters' drogues are centred at 15 m. ADCP data are from O.R.V. *Franklin* cruises Fr95/3, Fr95/8, and Fr96/6 and are averaged between 20 m and 28 m depth for 20 minutes. Corresponding 'model' estimates for the time and place of the observations are plotted on the *y* axis. The 'model' is the sum of the satellite altimetric velocity, the mean velocity for 1992–1998 from the ACOM3 global model, and a simple Ekman layer model driven by daily NCEP Reanalysis winds. Root-mean-squares of observed, modelled, and error velocities are given, as well as correlation and regression coefficients ('*r*' and 'slope', respectively).

variance ($r^2 = 0.5$) of the drifter and ADCP velocities, and included a systematic underestimation (slope = 0.4 for u and 0.47 for v) by about a half, although the observed peak velocities of 1.3 m s^{-1} were well represented. The underestimation was due to smoothing of the true field by the sea-level gridding procedure and gradient determinations.

The contribution to the total velocity by the transient geostrophic currents was so great that errors of the mean field or Ekman-layer model were difficult to determine from drifter and ADCP observations, even when 13 882 velocity observations were available. It was therefore not obvious which of our two estimates of the mean flow was correct or whether the parameters of the Ekman-layer model were optimal.

It was difficult to calibrate our surface wind-drift velocity estimate, which required detailed knowledge of the near-surface drift characteristics of larvae. The WOCE SVP drifters were drogued from 10 to 20 m and hence were unsuitable unless the drogues became unattached, and even then they would have had different drift characteristics.

We also compared our velocity estimates with six years of NOAA AVHRR images of sea surface temperature that were viewed as an animation. The comparison was encouraging, although difficult to quantify (Anon. 2001). The altimetric estimates were a smoothed version of reality, but most major flows were represented, and no 'spurious' eddies or currents occurred. Plate II shows one example image. Including drifters in the animation showed that position errors were relatively small; their motion agreed better with the sea-surface temperature maps than did the altimetric estimates. The drifters often travelled along sharp temperature fronts. For example, note the sharp temperature front along 29°S between 110°E and 112°E . It appeared to result from a branch of the Leeuwin Current, which was heading seaward from the continental slope along 28°S , riding over northward flow that must have been associated with a gradient between high sea level at 29.5°S , 110°E , and low sea level at 29.5°S , 112.5°E . The altimetric velocity field lacked sharp frontal features like this one but did have the general sense of the circulation correct, even at the mesoscale, which was a major advance over that possible without altimetry.

Unresolved random velocities $\mathbf{v}_{rand}$

From Fig. 3, the unresolved variance of the observations had a root-mean-square value of about 0.2 m s^{-1} . Some of these errors were associated with failure of our model to represent sharp frontal features, but many were due to an absence of small-scale turbulence—hence the need for additional random velocities $\mathbf{v}_{rand}$ in Eq. 2... 4 to bring the total modelled velocity variance closer to that of the observations. As a first step toward correctly simulating the error-covariance time and length scales, we added independent random velocities of root-mean-squared amplitude 0.05 m s^{-1} to the altimetric velocity grid (20 km, 5 d) and 0.1 m s^{-1} at the individual tracked-particle level (any separation, every 8 h).

Year classes modelled

We simulated the fate of six year classes after the launch of Topex/Poseidon. The first of these year classes, which resulted from hatchings over the 1992–1993 summer, was the 1993 year class. The last was the 1998 year class, whose tail end of modelled settlement was missing because we had not yet processed all data streams for 1999.

Results

The complete larval-advection model had more than 20 important parameters. We focused on the intra- and interannual results of a model run that used the parameter values discussed above and the mean field of the global

circulation model. Next, we discuss the impact of varying those parameters on model results.

A sequence of snapshots of the positions of model larvae for the 1995 year class is shown in Plate III. The striking feature of this simulation is that most of the model larvae remained within the latitudinal range of the adults, at least by the beginning of May. Most of the early-stage larvae leaving the model domain by May did so to the north or west. The north-westward influence of the strong summer southerly winds was largely, but not completely, countered by the eastward and southward influence of the geostrophic current. Model larvae taken north of 23°S had little chance of returning.

The distribution of model larvae in July was broadly consistent with the June–July distribution observed by Phillips (1981).

By September, the balance had shifted as the winds south of 30°S had swung around to westerlies, the south-easterlies north of 30°S had weakened, the Leeuwin Current had passed through its period of maximum flow, and larvae were at greater depth. Many model larvae rounded Cape Leeuwin by September. Very few returned. This result appears unlikely because puerulus settlement is minimal at Cape Mentelle, but the greatest observed settlement at Cape Mentelle was in years of strong Leeuwin Current.

In addition to a general northwards then southwards oscillation, a westward spread of the model larvae with time occurred, which was not simply due to the wind. The velocities associated with the mesoscale eddy field were typically 10 times those of the mean geostrophic field or wind. Consequently, larvae were constantly changing relative position within the population and diffusing away from their origin. The distribution, at any instant, of the individuals destined to 'settle' (shown in red in Plate III) was patchy but essentially random throughout the range (23°S – 35°S) of the population.

The offshore extent (Fig. 4) of larvae that eventually settled was less distinct. Some model larvae returned from as far west as 105°E , a distance of more than 1000 km, but many more achieved only 600 km.

One consequence of the vigorous mixing by the eddy field was that the probability of eventually settling was independent of hatching latitude (Fig. 5). This independence was apparently a consequence of the mesoscale eddy field, which we discerned by experimentally setting the altimetric velocities to zero in the model (Plate IV). Note how the red, eventually settling, model larvae were tightly clustered. Despite the clustering and a shoreward jet near the Abrolhos Islands, they did not settle within the same area; settlement remained broadly distributed. Settled individuals were mostly hatched near the Abrolhos Islands, as in the other years (Fig. 6), suggesting that, were it not for mixing by eddies, the Abrolhos Islands would be the optimal spawning location. In no experiment was hatching date important.

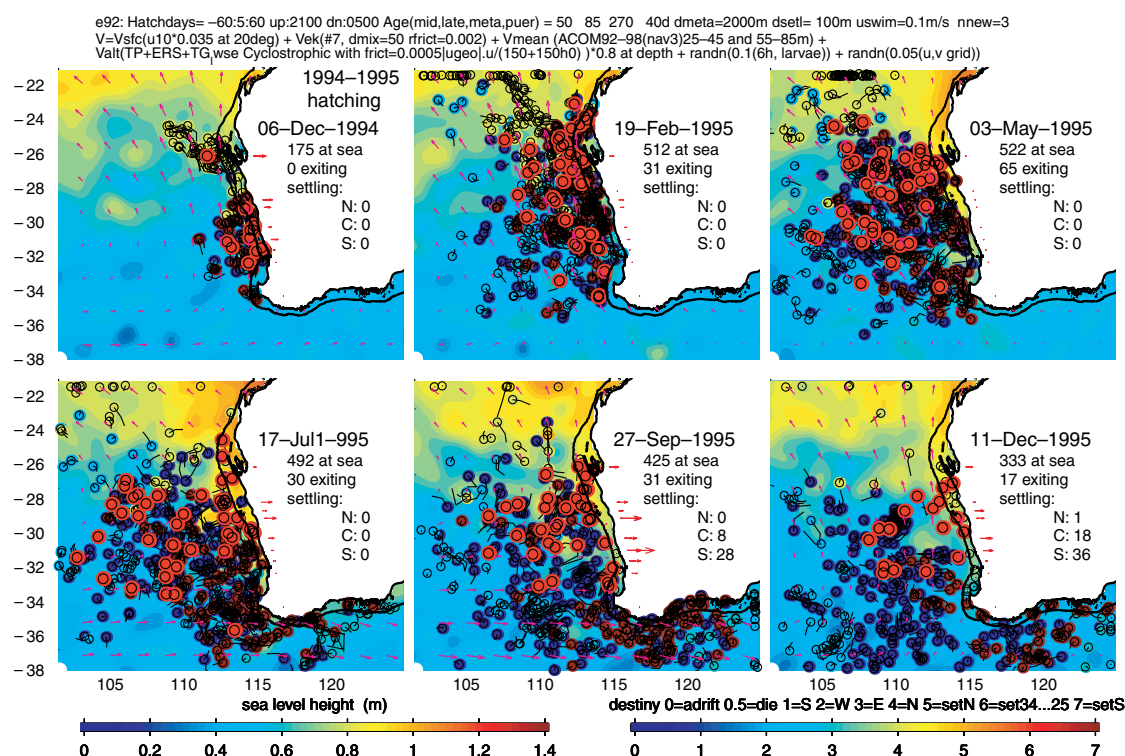


Plate III. Modelled fate of the 1995 year class. Positions of model larvae shown at 73-day intervals, from 30 days after the first larvae are released to one year later. Tails indicate trajectories over the previous 5 days. Larvae are colour-coded by their eventual destiny, red indicating the individuals that subsequently 'settle' (see text) within the fishery (34°S-25°S). The number of these, as well as how many settle north (N:) and south (S:) of the fishery, is shown in each panel along with the number still at sea and the number leaving the system since the previous panel. Positions at which larvae left are marked with open circles. The background colour field shows the interval-averaged altimetric sea-level height anomaly about the 1993-98 mean, plus the climatological surface dynamic height with respect to 300 m. Magenta arrows show the interval-averaged NCEP/NCAR wind stress. Red arrows on the land at the latitudes of coastal collectors indicate the observed rates of puerulus settlement. Model parameters are listed along the top.

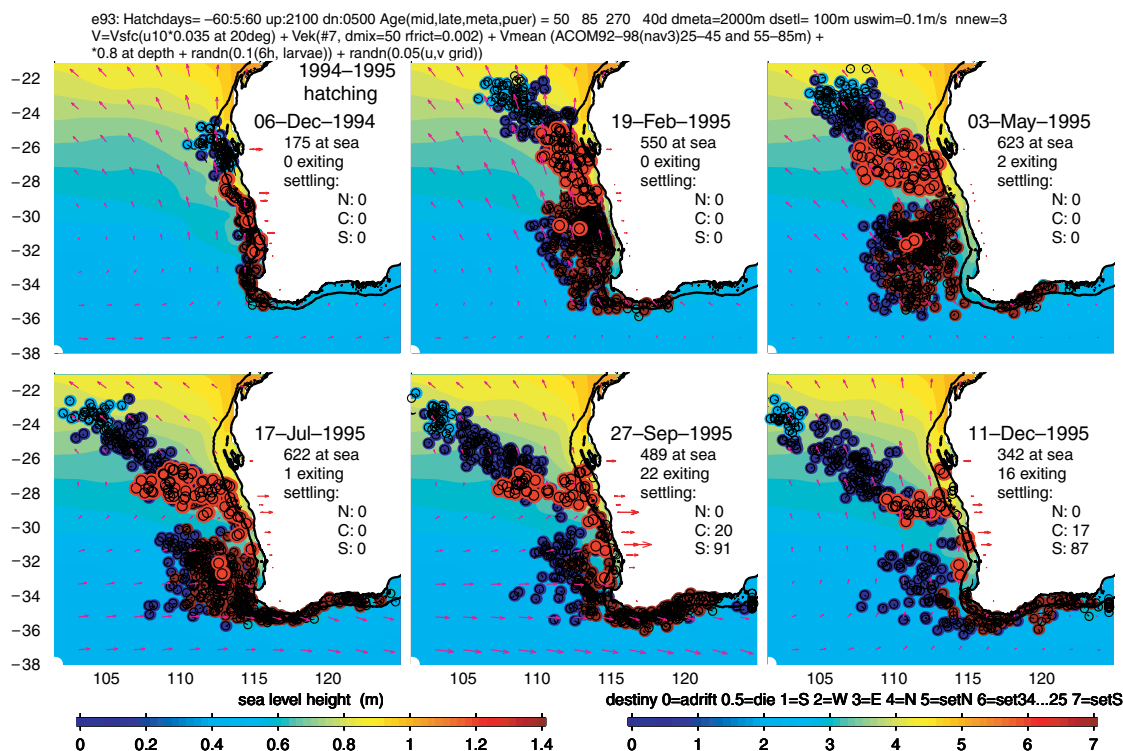


Plate IV. As for Plate III except that the altimetric velocity is set to zero in the model, leaving only the mean, wind-driven, and random (see Eqs 2... 4) velocity components. The climatological mean surface dynamic height with respect to 300 m is shown.

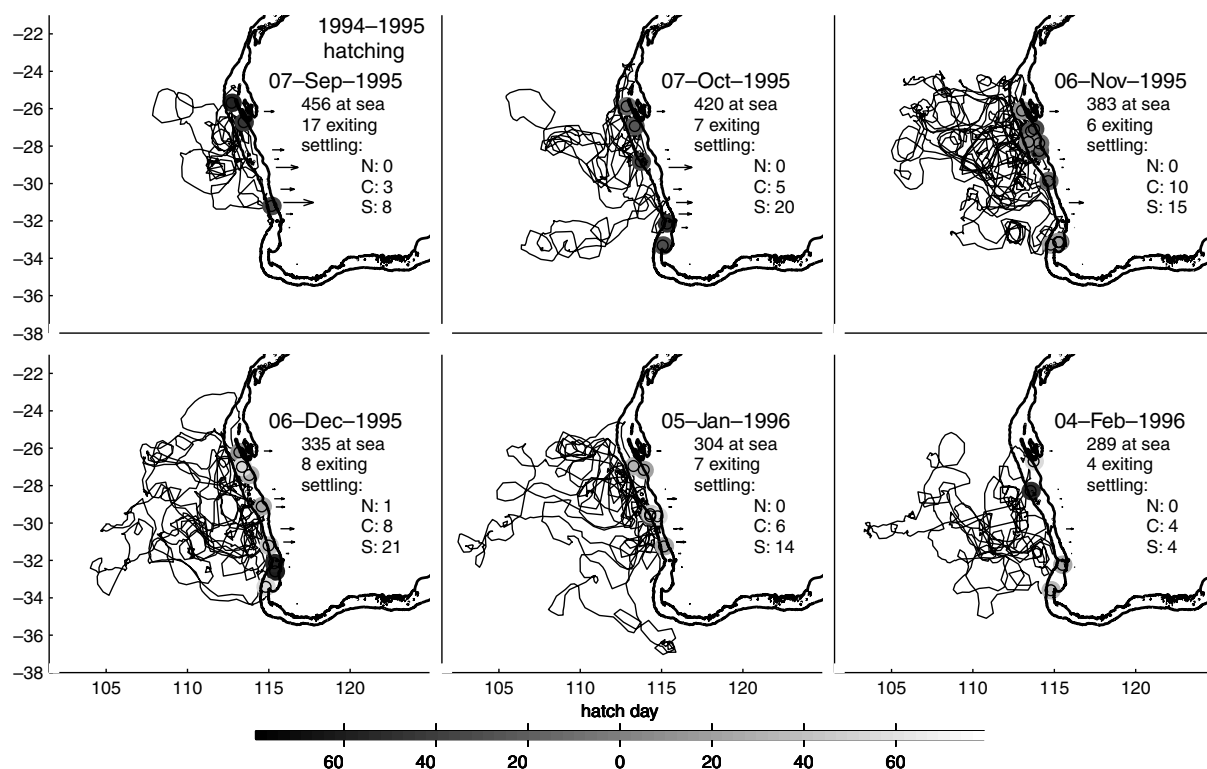


Fig. 4. Trajectories of those model larvae that return to the fishery. Each panel shows the complete trajectory from hatching to settlement of just those larvae settling in the central region (34°S–25°S) during the month prior to the panel date. The arrival point on the shelf is shown as a circle shaded to indicate the hatch day (0 = 1 January) of the larva. Arrows on the land at the latitudes of coastal collectors indicate the observed rates of puerulus settlement during the same period.

Although eddies were responsible for mixing at one length scale, they might also be agents of antidiffusion at a smaller scale, as shown when a real drifter (WOCE drifter 6152) became trapped in a cyclonic eddy (with a central depression of 0.3 m) at 33°S, 113°E, on 5 September 1995 (Anon. 2001). The drifter remained in the eddy for at least 225 days; the data record ended at 34°S 105.5°E. Inclusion of the small amount of interfacial drag in Eqs 5 and 6 was enough to make the surface field sufficiently convergent for model larvae to be significantly associated with cyclonic eddies, rather than with anticyclonic eddies. Such a phenomenon, if it occurs in nature, could have a significant impact on larval mortality, because the two eddy environments potentially differ greatly in prey field. Inspection of SeaWiFS chlorophyll-*a* estimates for 1997–1999 (Plate I; Anon. 2001) showed that cyclonic eddies had no surface expression in chlorophyll *a*, whereas the anticyclonic eddies of shelf waters shed by the Leeuwin Current were higher in chlorophyll *a*. Cyclonic eddies may, however, have significant productivity at depth that is not detected by satellite (Millan-Nunez *et al.* 1997).

Interannual variability

The number of model larvae settling each year was relatively constant (Fig. 5), compared with the fivefold

difference between the observed puerulus settlements of 1996 and 1993 (Fig. 1). The modelled settlement was not correlated with the observations, and the ranking of the model years was sensitive to small changes of many of the model parameters. Even rerunning the model with no changes other than the random velocities could reorder the settlement rates. Some model runs gave settlement rates that were correlated with the observed interannual variability, but no model runs gave the large observed differences between years.

The only model statistics that varied robustly from year to year were the number of model larvae leaving the model domain to the north (which happened early in the year) and the number rounding Cape Leeuwin and leaving to the east (later in the year). For example, in 1993, 40% of the year class (which was twice the usual number) of larvae left to the north as a consequence of the weakened geostrophic flow that was indicated by low sea levels (Fig. 1). Summer south-easterly winds of early 1993 were no stronger than usual. Loss of larvae around Cape Leeuwin was negatively correlated with loss to the north. In 1996, 40% of the year class (again twice the usual number) were lost around Cape Leeuwin, and again, this loss was associated with an anomalous (strong) Leeuwin Current, as indicated by high sea level (Fig. 1). The wind in 1996 had an anomalously

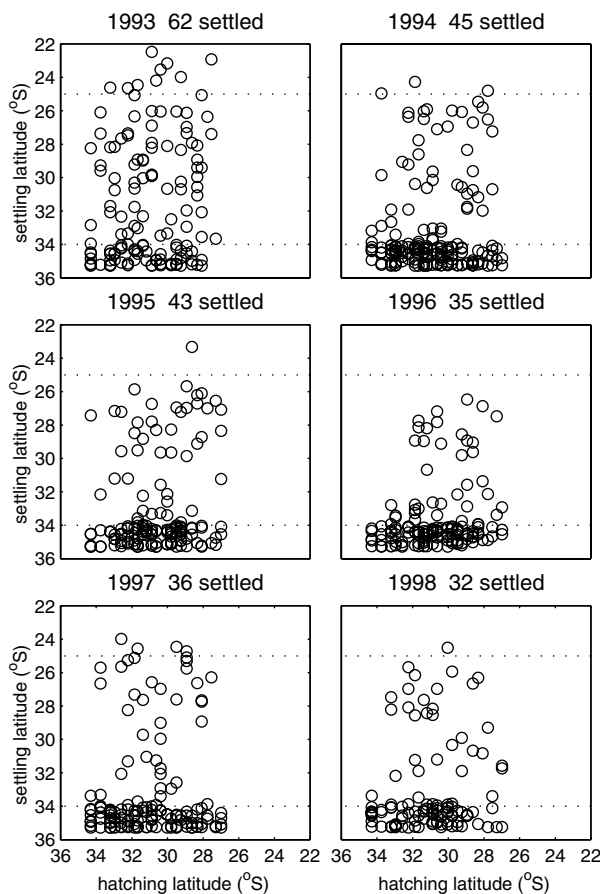


Fig. 5. Settling latitude versus hatching latitude of individual model larvae. The total number settling (of 625 released) within the fishery (between 34°S and 25°S, and west of 117°E) is shown for each year.

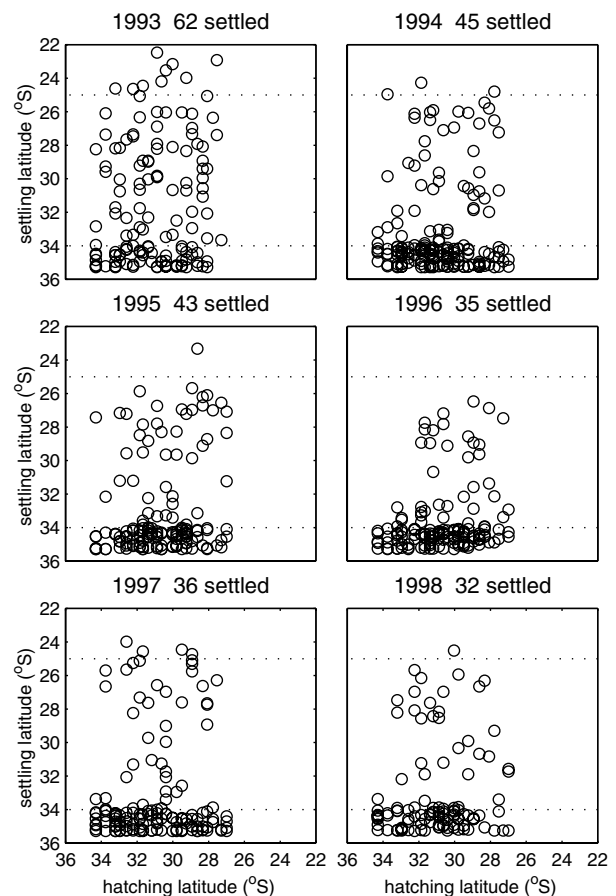


Fig. 6. As for Fig. 5 but with the altimetric velocity set to zero in the model.

strong eastward component that drove a northward Ekman flux and north-eastward surface current. The effect on the model larvae was to keep them closer to the continental shelf, where the strongest southward flow occurred.

The number of late-stage model larvae left in the middle, adjacent to the adult population, was therefore relatively constant from year to year, as reflected, albeit more noisily, in the number of larvae modelled as settling.

The time scale over which all model larvae either left the model domain or settled was such that settlement of year classes did not overlap, except in 1994 when larval loss due to advection was so low that modeled puerulus settlement in 1995 was potentially augmented by settlement of the 1994 year class. However, the model explicitly excludes all other causes of larval loss such as predation and starvation, which might reduce the effect of prior year classes.

Sensitivity of results to parameter uncertainty

The observed rate of puerulus settlement in 1995 and 1996 was very high, but these were years when the model showed many larvae rounding Cape Leeuwin. We might have been

overestimating the strength of the Leeuwin, underestimating the effect of the summer surface wind drift northward, or underestimating the depth to which mid- and late-stage larvae descend by day, but recall that the 'standard' model run employed the mean flow estimated by the global ocean model. If we instead used the mean flow computed from the hydrographic climatology, relative to either 300 or 1000 m, modelled and observed settlement rates were still uncorrelated, although the numbers leaving the model domain were slightly lower.

Increasing the surface wind-drift factor from 3.5 to 5% significantly reduced the number of larvae rounding Cape Leeuwin and increased the numbers leaving to the north and west, which were insignificant for the standard run. The numbers remaining in the middle and settling were lower and still constant from year to year. Conversely, reducing the surface wind-drift factor to 2% slightly increased the number rounding Cape Leeuwin, at the expense of the number going north.

Increasing the mean depth to which mid- and late-stage larvae descended by day from 70 m to 100 m had essentially

no impact, perhaps because the global model does not resolve the shear. Using the deeper hydrographic mean current field also had little influence. Attenuating the altimetric current at depth by 0.5 instead of 0.8 did not reduce the losses around Cape Leeuwin.

The importance of vertical migration

To investigate the importance of diurnal vertical migration, we performed experiments in which model larvae ascended for 0 or 16 h (instead of 8 h for the standard run). In the 0 h run, half (instead of 10%) of the model larvae rounded Cape Leeuwin by July under the influence of the Leeuwin Current. In the 16-h run, half (instead of 15%) of the model larvae left the model domain to the north or west by April. The fraction of time spent near the surface was therefore a parameter to which the trajectories of the model larvae were very sensitive.

Metamorphosis and swimming

No experiments with the parameters controlling metamorphosis and settlement made significant changes to the interannual variations of modelled settlement. The eastward swimming speed (0.1 m s^{-1}) of the model pueruli was enough to give them an approximately 50% chance, for each year modelled, of reaching the 100-m isobath within one week.

Discussion

The present work was motivated by a desire to explore the hypothesis that interannual variations of transport of the phyllosoma larvae were responsible for the observed correlation of coastal sea level with puerulus settlement. For our simulations, we used the most accurate velocity fields available, as distinct from the most detailed, which might be provided by a high-resolution hydrodynamic model. The benefit of our approach was that the temporal variability of both the large-scale flows and mesoscale eddies was well represented for the particular year classes simulated. The principal drawback of this method, however, was that our representation of vertical shear was fairly crude, although we doubt it was limiting, given the gaps in our knowledge of the vertical migration behaviour of the larvae. The altimetric analysis had other weaknesses. One was that the flows over the continental shelf, especially the across-isobath component, were poorly represented. We think that this failing was unlikely to be limiting the model, compared with the crude algorithm for triggering metamorphosis to the puerulus. Poor resolution of sharp fronts was another weakness, the consequence of which was hard to anticipate because it depended on whether the diurnal migrations of real larvae result in their crossing fronts.

The impact of the large sea-level anomalies occurring during our study period was evident in the flow fields and subsequent movement of model larvae, but the number of

late-stage larvae being transported to the shelf edge around the time of settlement did not vary as much from year to year as did natural settlement on coastal collectors. The presently modelled settlement rate would be better correlated with observations only if the number of model larvae carried around Cape Leeuwin were lower in years of strong Leeuwin Current. The losses to the north in years of weak flow would then generate variability that would be correlated with observed settlement.

We conclude therefore that, unless phyllosoma larvae have a way of escaping advection around Cape Leeuwin, variability of advection of larvae is not the dominant process controlling variability in puerulus settlement along the coast. We surmise that the controlling factor is one that is correlated with sea level and was not included in the model, such as temperature, which affects hatching (Aldrich, 1967), growth rate, and survival (Chittleborough and Thomas, 1969; Marinovic 1996) and is correlated with both sea level and puerulus settlement (Caputi *et al.* 2001 this issue). Earlier hatching and faster development of larvae when the water is warmer would favour metamorphosis and settling of a greater proportion before they were carried south by the current. The advent of quantitative ocean-colour imagery in 1997 permits a representation of prey density also to be included in a model, once the relationship of surface chlorophyll *a* with the feeding-depth abundance of preyed-upon creatures (which must be identified) is known (if indeed there is one). Inspection of the few available years of SeaWiFS ocean-colour images shows that, although the winter chlorophyll-*a* density varied little from year to year, the density during the El Niño summer of 1997–98 was low (see Fig. 1), potentially explaining the very low settlement rate in 1998 and encouraging further study.

The present model included numerous other simplifications, and it is hard to know which was primarily responsible for its failure to reproduce the observed extent of interannual variability of puerulus settlement. One of these deficiencies was our lack of understanding of the cue to metamorphose from the final phyllosoma larval stage to the puerulus. Field studies of puerulus abundance are confounded by the strong currents over the continental slope, such that recently metamorphosed pueruli occurring far offshore did not necessarily metamorphose there or even in that water mass. Velocities of up to 1.5 m s^{-1} either shoreward or seaward must be factored into the model to permit back-calculation of the location of metamorphosis.

Notwithstanding the model's deficiencies, its results were consistent with observed survival patterns, without 'tuning' of its parameters away from literature-based estimates. The observed vertical migration balanced the north- and westward influence of the wind against the south- and eastward influence of the geostrophic flow. This is essentially the balance that has generally been assumed to exist (*e.g.* Pearce and Phillips 1994) but that has not

previously been evaluated quantitatively. We are not aware, in fact, of any species with such an extended pelagic larval phase for which the mechanism for retention of a large proportion of hatched larvae within the range of the species has been quantitatively evaluated.

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References

- Aldrich, F. (1967). Observations by the late F. Aldrich on Australian marine crayfish in captivity. *Western Australian Naturalist* **10**, 162–68.
- Andrews, J. C. (1983). Ring structure in the poleward boundary current off western Australia. *Australian Journal of Marine and Freshwater Research* **34**, 547–61.
- Anon. (2001). WA [Western Australia] ocean movies 1993–2000. CD-ROM version 3. 4. (CSIRO Marine Research: Hobart.)
- Caputi, N., Fletcher, W. J., Pearce, A. F., and Chubb, C. F. (1996). Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the west Australian coast. *Marine and Freshwater Research* **47**, 147–55.
- Caputi, N., Chubb, C., and Pearce, A. (2001). Environmental effects on recruitment of the western rock lobster, *Panulirus cygnus*. *Marine and Freshwater Research* **52**, 1167–74.
- Chiswell, S. M., and Booth, J. D. (1999). Rock lobster *Jasus Edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Marine Ecology Progress Series* **183**, 227–40.
- Chittleborough, R. G., and Thomas, L. R. (1969). Larval ecology of the western Australian marine crayfish, with notes upon other panulirid larvae from the eastern Indian Ocean. *Australian Journal of Marine and Freshwater Research* **20**, 199–223.
- Chubb, C. F. (1991). Measurement of spawning stock levels for the western rock lobster, *Panulirus cygnus*. *Revista de Investigaciones Marinas* **12**, 223–33.
- Cresswell, G. R., and Golding, T. J. (1980). Observations of a south-flowing current in the southeastern Indian Ocean. *Deep Sea Research* **27A**, 449–66.
- Godfrey, J. S., and Ridgway, K. R. (1985). The large-scale environment of the poleward-flowing Leeuwin Current, western Australia: longshore steric height gradients, wind stresses and geostrophic flow. *Journal of Physical Oceanography* **15**, 481–95.
- Griffin, D. A., and Middleton, J. H. (1991). Local and remote wind forcing of New South Wales inner shelf currents and sea level. *Journal of Physical Oceanography* **21**, 304–22.
- Hamon, B. V., and Cresswell, G. R. (1972). Structure functions and intensities of ocean circulation off east and west Australia. *Australian Journal of Marine and Freshwater Research* **23**, 99–103.
- Hofmann, E. E., Hedstrom, K. S., Moisan, J. R., Haidvogel, D. B., and Mackas, D. L. (1991). Use of simulated drifter tracks to investigate general transport patterns and residence times in the coastal transition zone. *Journal of Geophysical Research* **96**, 15041–52.
- Ince, L. S., and Naimie, C. E. (2000). Modelling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. *Fisheries Oceanography* **9**, 99–113.
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R., and Joseph, D. (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society* **77**, 437–71.
- Katz, C. H., Cobb, J. S., and Spaulding, M. (1994). Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. *Marine Ecology Progress Series* **103**, 265–73.
- Lemmens, J. W. T. J. (1994). Biochemical evidence for absence of feeding in puerulus larvae of the western rock lobster *Panulirus cygnus* (Decapoda: Palinuridae). *Marine Biology* **118**, 383–91.
- Le Traon, P. -Y., and Hernandez, F. (1992). Mapping the oceanic mesoscale circulation: validation of satellite altimetry using surface drifters. *Journal of Atmospheric and Oceanic Technology* **9**, 687–98.
- Marinovic, B. B. (1996). Behavioural and physiological investigations with respect to light and temperature on the phyllosoma larvae of the western rock lobster *Panulirus cygnus* George, 1962. Ph.D. Thesis, University of Western Australia, Crawley.
- Millan-Nunez, R., Alvarez-Borrego, S., and Trees, C. C. (1997). Modeling the vertical distribution of chlorophyll in the California Current system. *Journal of Geophysical Research* **102**, 8587–95.
- Pearce, A. F., and Griffiths, R. W. (1991). The mesoscale structure of the Leeuwin Current: a comparison of laboratory model and satellite images. *Journal of Geophysical Research* **96**, 16739–57.
- Pearce, A. F., and Phillips, B. F. (1988). ENSO events, the Leeuwin Current, and larval recruitment of the western rock lobster. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **45**, 13–21.
- Pearce, A. F., and Phillips, B. F. (1994). Oceanic processes, puerulus settlement and recruitment of the western rock lobster *Panulirus cygnus*. In 'The Bio-physics of Marine Larval Dispersal.' Coastal and Estuarine Studies 45. (Eds P. W. Sammarco and M. L. Heron.) pp. 279–303. American Geophysical Union: Washington, D. C.)

- Phillips, B. F. (1975). 'The Effect of Water Currents and the Intensity of Moonlight on Catches of the Puerulus Larval Stage of the Western Rock Lobster.' Report of the Division of Fisheries and Oceanography, CSIRO Australia, No. 63. 8 pp.
- Phillips, B. F. (1981). The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. *Oceanography and Marine Biology Annual Review* **19**, 11–39.
- Phillips, B. F. (1986). Prediction of commercial catches of the Western Rock Lobster *Panulirus cygnus* George. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2126–30.
- Phillips, B. F., and Olsen, L. (1975). Swimming behaviour of the puerulus larvae of the Western Rock Lobster. *Australian Journal of Marine and Freshwater Research* **26**, 415–57.
- Phillips, B. F., and Pearce, A. F. (1997). Spiny lobster recruitment off Western Australia. *Bulletin of Marine Science* **61**, 21–41.
- Phillips, B. F., Rimmer, D. W., and Reid, D. D. (1978). Ecological investigations of the late-stage phyllosomata and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. *Marine Biology* **45**, 347–57.
- Pollard, R. T., and Millard, R. C. (1970). Comparison between observed and simulated wind-generated inertial oscillations. *Deep-Sea Research* **17**, 813–21.
- Polovina, J. J., Kleiber, P., and Kobayashi, D. R. (1999). Application of Topex/Poseidon satellite altimetry to simulate transport dynamics of larvae of the spiny lobster (*Panulirus marginatus*), in the northwestern Hawaiian Islands, 1993–96. *Fisheries Bulletin, U.S.*, **97**, 132–43.
- Rimmer, D. W., and Phillips, B. F. (1979). Diurnal Migration and vertical distribution of phyllosomata larvae of the western rock lobster *Panulirus cygnus*. *Marine Biology* **54**, 109–24.
- Rimmer, D. W. (1980). Spatial and temporal distribution of early-stage phyllosomata of western rock lobster, *Panulirus cygnus*. *Australian Journal of Marine and Freshwater Research* **31**, 485–97.
- Ritz, D. A. (1972). Factors affecting the distribution of rock-lobster larvae (*Panulirus longipes cygnus*), with reference to variability of plankton-net catches. *Marine Biology* **13**, 309–17.
- Schiller, A., Godfrey, J. S., McIntosh, P. C., Meyers, G., and Fiedler, R. (2000). Interannual dynamics and thermodynamics of the Indo-Pacific Oceans. *Journal of Physical Oceanography* **30**, 987–1012.